

# Molecular phylogeny reveals a new genus and species of freshwater mussel (Bivalvia, Unionidae, Gonideinae) from Jiangxi, China

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<https://zoobank.org/6BD143C1-F9E5-4685-9B80-857CDDB788AD>

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Academic editor: Matthias Glaubrecht ♦ Received 21 August 2024 ♦ Accepted 1 October 2024 ♦ Published 22 October 2024

## Abstract

Freshwater mussels of the tribe Gonideini (Bivalvia: Unionidae: Gonideinae) constitute one of the most taxonomically diverse groups and serve as keystone species in riverine and lacustrine ecosystems across East Asia. A new genus and species of Gonideini (Bivalvia: Unionidae) is described from Jiangxi, China, as *Pseudopostolata angula* **gen. et sp. nov.** based on an integrative analysis of shell morphology and molecular data. The validity of the new genus and species is supported by distinct conchological features: a short, rounded anterior; a long, wide posterior; a slightly downward-curved dorsal margin; and a distinctly obtuse angle at the center of the posterior margin. The multi-locus (*COI* + *16S* rRNA + *28S* rRNA) phylogeny showed that the species formed a monophyletic group in the tribe Gonideini of the subfamily Gonideinae. *Pseudopostolata angula* **gen. et sp. nov.** is identified as the sister group to a clade comprising the genera *Postolata*, *Cosmopseudodon*, *Obovalis*, *Ptychorhynchus*, *Parvasolenaia*, and *Koreosolenaia*. We emphasize the significant morphological convergence in freshwater mussels, particularly within Gonideini, highlighting the necessity of an integrated taxonomic approach for accurate generic classification of this group.

## Key Words

Gonideini, molecular systematics, morphological characters, taxonomy

## Introduction

The Unionida, a group of freshwater mussels, is the most species-diverse among the freshwater bivalve, comprising approximately 192 genera and 958 of the more than 1,200 existing species (Graf and Cummings 2021). North America, as well as eastern and southeastern Asia, represent two major hotspots of unionid bivalve diversity (Haag 2012; Zieritz et al. 2018). Recent research efforts have concentrated on the Unionida fauna of China, encompassing extensive specimen collection and DNA sequencing. These endeavors have led to a notable expansion in the documented diversity of Unionida species in the region, along with the identification of numerous new taxa (Wu et al. 2022, 2023, 2024; Chen et al. 2023; Dai

et al. 2023, 2024a, 2024b; Liu et al. 2024). The majority of these taxonomic changes were from Southern China. This indicates that the diversity of species in South China may be significantly underestimated, particularly in creeks that have not been previously studied (Dai et al. 2023). Many freshwater mussel populations have rapidly declined because of different factors such as pollution, water quality degradation, habitat destruction or alteration, and invasive species (Haag 2012; Aldridge et al. 2022; Sousa et al. 2022). Consequently, research and conservation efforts for this community are receiving greater attention, underscoring the imperative to describe species diversity and systematics in previously unstudied areas (Huang et al. 2019; Chen et al. 2023; Dai et al. 2023; Zieritz et al. 2024).



Gonideini Ortmann, 1916, within the subfamily Gonideinae of the family Unionidae, represents one of the most taxonomically diverse groups of freshwater mussels in East Asia. At least 12 genera of 33 valid species are recognized, with more than half distributed in China (MUSSEL Project Database, see <http://mussel-project.uwsp.edu/>). Notably, *Postolata* Dai, Huang, Guo & Wu, 2023 is endemic to China. Gonideini species are distinguished by their trapezoidal to rectangular shells, the absence or presence of only vestigial hinge teeth, and a tetragenous brooding type (Lopes-Lima et al. 2017; Froufe et al. 2020). Nevertheless, the shell morphology exhibits significant phenotypic plasticity and convergence, making it difficult to classify based solely on morphological traits reliably (Zieritz and Aldridge 2009; Inoue et al. 2013). This is particularly pronounced in Gonideini. In the tribe Gonideini, the four species of the genus *Sinosolenia*, except *Sinosolenia carinata* (Heude, 1877), exhibit a high degree of convergence. Moreover, the morphology of *Ptychorhynchus* Simpson, 1900, *Postolata* Dai, Huang, Guo, and Wu, and *Obovalis* Simpson, 1900, displays notable similarities (Dai et al. 2023). An integrative approach, encompassing both morphological and molecular characterization, is a relatively straightforward and precise method for classifying freshwater mussels (Smith et al. 2019; Bolotov et al. 2020a, 2023).

In the present study, we found a unique freshwater mussel species from Wujiang River, Ji'an City, China. Morphological and molecular evidence supported these loach specimens as a new genus and a new species in the

tribe Gonideini of the subfamily Gonideinae. Hence, the new genus and species *Pseudopostolata angula* gen. et sp. nov. are described herein. Furthermore, the phylogenetic relationships within Gonideini are discussed.

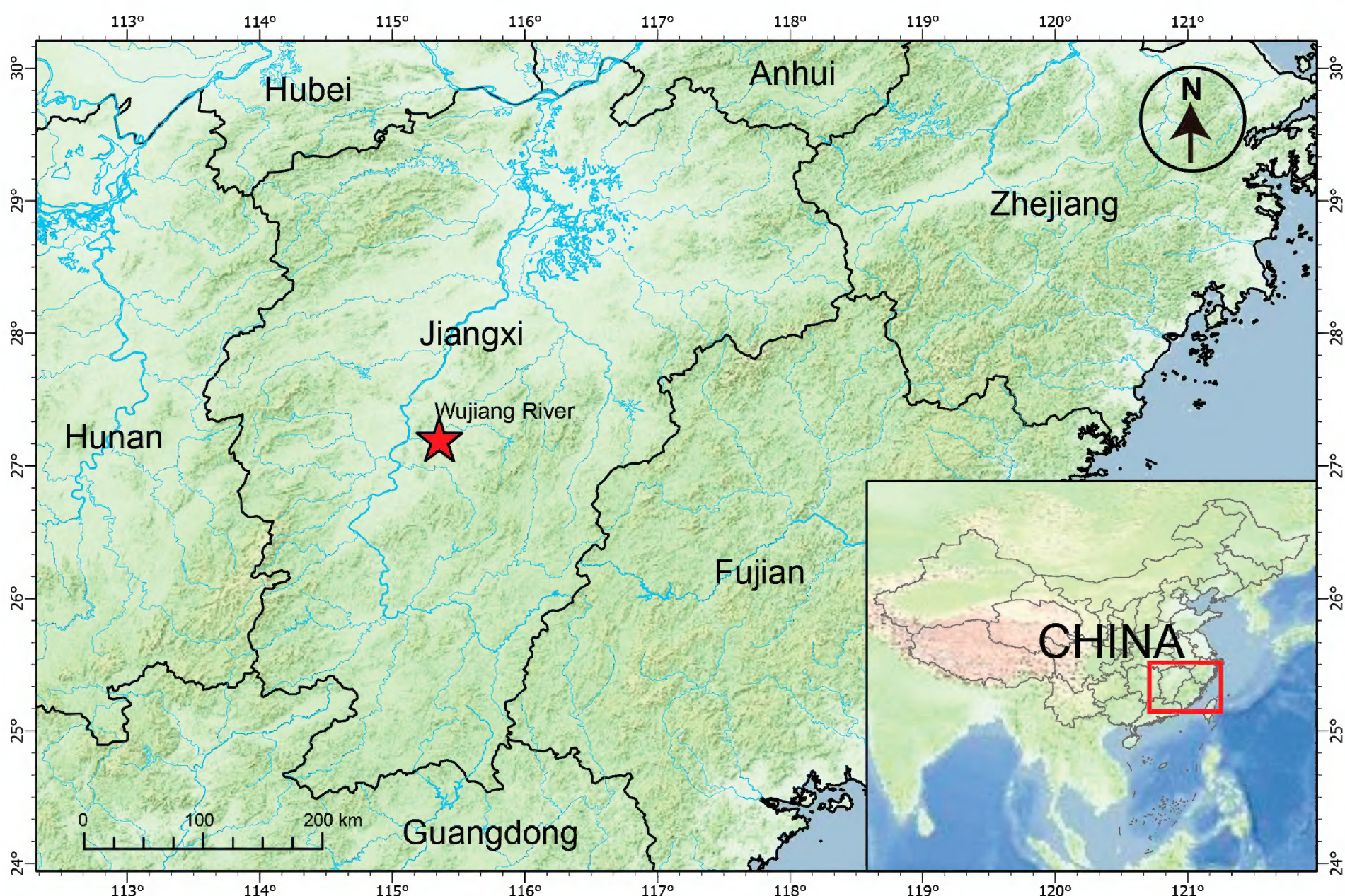
## Materials and methods

### Specimen sampling, identification, and deposition

In December 2023, eight specimens were collected from the Wujiang River (27°03'37"N, 115°42'17"E) in Ji'an City, Jiangxi Province, China (Figs 1, 2, 4). A digital vernier caliper with an accuracy of  $\pm 0.01$  mm was used to measure the length, height, and width of the type series for the new taxa. Live specimens were euthanized with 100% ethanol and then separated into soft tissue and shell. The adductor muscle was used for DNA extraction, while the remaining soft tissue was preserved at  $-80^{\circ}\text{C}$ . All voucher specimens were deposited in the Museum of Biology, Nanchang University (NCUMB), China.

### Molecular phylogenetic analyses

The Qiagen Genomic DNA Kit (Qiagen, Hilden, Germany) was employed to extract total genomic DNA from the excised tissue following the instructions provided by the manufacturer. The quality and concentration of the DNA were checked on 1% agarose gel electrophoresis and NanoDrop 2000 (Thermo Scientific, USA).



**Figure 1.** Distribution map of *Pseudopostolata angula* gen. et sp. nov.





**Figure 2.** The type locality and shell morphology of *Pseudopostolata angula* gen. et sp. nov. **A, B.** General view of the type locality, Wujiang River, Ji'an City, Jiangxi Province, China; **C, D.** Shell morphology of *Pseudopostolata angula*.

We amplified and sequenced fragments from the mitochondrial cytochrome c oxidase subunit-I gene (*COI*) (LCO22me2 + HCO700dy2) (Walker et al. 2007), *16S* small ribosomal RNA gene (*16S*) (16sar-L-myt + 16sbr-H-myt) (Bolotov et al. 2018), and nuclear *28S* ribosomal RNA gene (*28S*) (D23F + D4RB) (Park and Foighil 2000). The polymerase chain reaction (PCR) was conducted using a 25  $\mu$ L mixture of 2  $\times$  Taq Plus Master MixII (Vazyme, China) (12.5  $\mu$ L), ddH<sub>2</sub>O (9.5  $\mu$ L), 10  $\mu$ M primers (1  $\mu$ L each), and genomic DNA (1  $\mu$ L, about 100 ng/ $\mu$ L). Thermal cycling was

started at 98  $^{\circ}$ C for 10 s, followed by 35 cycles of 94  $^{\circ}$ C for 1 min, annealing at 50  $^{\circ}$ C for 1 min, extension at 72  $^{\circ}$ C for 1 min, and then a final extension at 72  $^{\circ}$ C for 7 min. The PCR products were sequenced commercially by Sangon Biotech (Shanghai, China). The newly obtained sequences have been deposited in GenBank (Tables 1, 2).

Two datasets were constructed in this study: (i) the *COI* dataset (46 sequences; 600 bp) (Table 1); (ii) the three-gene dataset (containing *COI*, *16S*, and *28S*; 60 sequences; 1,482 bp) (Table 2).



**Table 1.** List of sequences used in genetic distances (\*, sequenced in this study).

Species	COI GenBank accession no.	Locality
<i>Pseudopostolata angula</i> <b>gen. et sp. nov.</b>	PQ189757*	China: Jiangxi, Ji'an, Wujiang River
<i>Pseudopostolata angula</i> <b>gen. et sp. nov.</b>	PQ189758*	China: Jiangxi, Ji'an, Wujiang River
<i>Obovalis omiensis</i>	MT020684	Japan
<i>Obovalis omiensis</i>	LC518995	Japan: Gifu
<i>Obovalis omiensis</i>	LC518996	Japan: Kyoto
<i>Obovalis omiensis</i>	LC518997	Japan: Shiga
<i>Ptychorhynchus pfisteri</i>	MG463036	China: Jiangxi, Gan River
<i>Ptychorhynchus pfisteri</i>	MG463034	China: Jiangxi, Gan River
<i>Ptychorhynchus pfisteri</i>	MG463035	China: Hunan, Xiangyin
<i>Ptychorhynchus pfisteri</i>	MG933729	Dongting Lake, China
<i>Ptychorhynchus pfisteri</i>	MG933730	Dongting Lake, China
<i>Ptychorhynchus pfisteri</i>	KY067440	China
<i>Parvasolenia rivularis</i>	MG463100	China: Jiangxi, Gan River
<i>Parvasolenia rivularis</i>	MG463101	China: Jiangxi, Gan River
<i>Parvasolenia rivularis</i>	MG463098	China: Jiangxi, Gan River
<i>Parvasolenia rivularis</i>	MG463103	China: Jiangxi, Gan River
<i>Parvasolenia rivularis</i>	MG463102	China: Jiangxi, Gan River
<i>Parvasolenia rivularis</i>	MG463099	China: Jiangxi, Gan River
<i>Parvasolenia rivularis</i>	MG463104	China: Jiangxi, Gan River
<i>Koreosolenia sitgyensis</i>	MT020682	South Korea
<i>Koreosolenia sitgyensis</i>	MT020683	South Korea
<i>Postolata guangxiensis</i>	OP009379	China: Guangxi, Guilin, Luo Qing River
<i>Postolata guangxiensis</i>	OP009380	China: Guangxi, Guilin, Luo Qing River
<i>Postolata guangxiensis</i>	OP009381	China: Guangxi, Guilin, Luo Qing River
<i>Postolata guangxiensis</i>	OP009382	China: Guangxi, Guilin, Luo Qing River

Species	COI GenBank accession no.	Locality
<i>Postolata guangxiensis</i>	OP009383	China: Guangxi, Guilin, Luo Qing River
<i>Postolata guangxiensis</i>	OP009384	China: Guangxi, Guilin, Luo Qing River
<i>Postolata guangxiensis</i>	OP009385	China: Guangxi, Guilin, Luo Qing River
<i>Postolata longjiangensis</i>	PP786557*	China: Guangxi, Hechi, Longjiang River
<i>Postolata longjiangensis</i>	PP786557*	China: Guangxi, Hechi, Longjiang River
<i>Cosmopseudodon wenshanensis</i>	PP079444	China: Yunnan, Wenshan, Panlong River
<i>Cosmopseudodon wenshanensis</i>	PP079445	China: Yunnan, Wenshan, Panlong River
<i>Cosmopseudodon wenshanensis</i>	PP079446	China: Yunnan, Wenshan, Panlong River
<i>Cosmopseudodon wenshanensis</i>	PP079447	China: Yunnan, Wenshan, Panlong River
<i>Cosmopseudodon wenshanensis</i>	PP079448	China: Yunnan, Wenshan, Panlong River
<i>Cosmopseudodon wenshanensis</i>	PP079449	China: Yunnan, Wenshan, Panlong River
<i>Cosmopseudodon wenshanensis</i>	PP079450	China: Yunnan, Wenshan, Panlong River
<i>Cosmopseudodon wenshanensis</i>	PP079451	China: Yunnan, Wenshan, Panlong River
<i>Cosmopseudodon resupinatus</i>	PP079436	China: Guangxi, Hechi, Taohua River
<i>Cosmopseudodon resupinatus</i>	PP079437	China: Guangxi, Hechi, Taohua River
<i>Cosmopseudodon resupinatus</i>	PP079438	China: Guangxi, Hechi, Taohua River
<i>Cosmopseudodon resupinatus</i>	PP079439	China: Guangxi, Hechi, Taohua River
<i>Cosmopseudodon resupinatus</i>	PP079440	China: Guangxi, Hechi, Taohua River
<i>Cosmopseudodon resupinatus</i>	PP079441	China: Guangxi, Hechi, Taohua River
<i>Cosmopseudodon resupinatus</i>	PP079442	China: Guangxi, Hechi, Taohua River
<i>Cosmopseudodon resupinatus</i>	PP079443	China: Guangxi, Hechi, Taohua River

The *COI* sequences were codon-aligned by MUSCLE ver. 3.6 (Edgar 2004) implemented in MEGA ver. 10.1.6 (Kumar et al. 2018), whereas *16S* rRNA and *28S* rRNA were aligned in MAFFT ver. 7 (Katoh et al. 2019) using the Q-INS-i algorithm. We used Gblocks ver. 0.91b (Castresana 2000) to exclude ambiguous areas of the alignment for each gene. DnaSP ver. 6 (Rozas et al. 2017) was used to calculate the number of haplotypes. The best-fit model for each gene and gene partition was calculated by PartitionFinder2 ver. 2.3.4 (Lanfear et al. 2017), based on the corrected Akaike Information Criterion (AICc) and using a heuristic search algorithm. The program proposed the division of the concatenated dataset into four partitions, comprising partitions for the *16S* and *28S* genes and each of the three codon positions of the *COI* gene. The best-fit model was determined to be GTR + I + G for the first and second codon positions of *COI*, as well as for *16S* and *28S*, while GTR + G was selected for the third position of *COI*.

Inter- and intra-specific distances based on the *COI* dataset were calculated in MEGA X using the uncorrected *p*-distance. Standard error estimates were obtained by 1000 bootstrapping replicates.

Maximum likelihood (ML) analyses were performed in raxmlGUI ver. 2.0 (Edler et al. 2020) with the ML + rapid bootstrapping method and 1000 replicates. Bayesian inference (BI) analyses were conducted in MrBayes ver. 3.2.6 (Ronquist et al. 2012). Four simultaneous runs with four independent Markov Chain Monte Carlo (MCMC) were implemented for 10 million generations,

and trees were sampled every 1000 generations with a burn-in of 25%. The convergence was checked with the average standard deviation of split frequencies < 0.01 and the potential scale reduction factor (PSRF) ~ 1.

Results

Phylogenetic analyses

A total of two *COI* haplotypes, one *16S* haplotype, and two *28S* haplotypes were identified in the eight sequenced specimens from Ji'an, Jiangxi. The *COI* dataset had an aligned length of 600 characters, with 164 variable sites and 162 parsimony informative sites. After trimming and concatenation, the three-gene dataset consisted of 1,482 characters, including 603 bp from *COI*, 467 bp from *16S*, and 412 bp from *28S*. This combined dataset contained 600 variable sites and 538 parsimony-informative sites.

The ML and BI trees based on the three-gene dataset exhibited largely congruent topologies, except for the phylogenetic relationships within Lamprotulini (Fig. 3). Both the ML and BI trees display a node with polytomies in the tribe Gonideini due to low nodal support. In our multilocus phylogenetic analysis, all eight recognized tribes within the subfamily Gonideinae were recovered as monophyletic groups. Specimens from Jiangxi formed a robust monophyletic clade (BS/BPP = 97/1.00) in the tribe Gonideini that did not belong to any previously known species or



**Table 2.** List of sequences used in multi-locus phylogenetic analyses (\*, sequenced in this study).

Taxon	COI	16S rRNA	28S rRNA
<b>UNIONIDAE Rafinesque, 1820</b>			
<b>Gonodeinae Ortmann, 1916</b>			
<b>Gonideini Ortmann, 1916</b>			
<i>Obovalis omiensis</i>	MT020684	LC223994	MT020830
<i>Obovalis omiensis</i>	LC518995	LC223994	MT020830
<i>Obovalis omiensis</i>	LC518996	LC223995	LC519064
<i>Obovalis omiensis</i>	LC518997	LC519045	LC519065
<i>Ptychorhynchus pfisteri</i>	MG463036	KY067440	MG595564
<i>Ptychorhynchus pfisteri</i>	MG463034	KY067440	MG595563
<i>Ptychorhynchus pfisteri</i>	MG463035	KY067440	MG595562
<i>Parvasolenia rivularis</i>	MG463100	KX966393	MG595626
<i>Sinosolenia carinata</i>	MG463087	NC_023250	MG595616
<i>Sinosolenia oleivora</i>	MG463090	NC_022701	MG595617
<i>Sinosolenia iridinea</i>	MG463091	MT477834	MG595618
<i>Sinosolenia recognita</i>	MG463092	KY561653	MG595619
<i>Leguminaia wheatleyi</i>	MN402614	MN396725	MN396721
<i>Microcondylaea bonellii</i>	KX822652	KT966473	KX822609
<i>Gonidea angulata</i>	MN402615	MN396726	MN396722
<i>Koreosolenia sitgyensis</i>	MT020682	GQ451859	MT020817
<i>Postolata guangxiensis</i>	OP009379	OP020466	OP020470
<i>Postolata guangxiensis</i>	OP009380	OP020467	OP020470
<i>Postolata guangxiensis</i>	OP009381	OP020468	OP020470
<i>Postolata guangxiensis</i>	OP009382	OP020469	OP020471
<i>Postolata guangxiensis</i>	OP009383	OP020467	OP020472
<i>Postolata guangxiensis</i>	OP009384	OP020468	OP020470
<i>Postolata guangxiensis</i>	OP009385	OP020469	OP020471
<i>Postolata longjiangensis</i> *	PP786557	PP786405	PP786407
<i>Postolata longjiangensis</i> *	PP786557	PP786406	PP786407
<i>Postolata longjiangensis</i> *	PP786558	PP786405	PP786407
<i>Postolata longjiangensis</i> *	PP786558	PP786406	PP786407
<i>Pseudopostolata angula</i> <b>gen. et sp. nov.*</b>	PQ189757	PQ201945	PQ201943
<i>Pseudopostolata angula</i> <b>gen. et sp. nov.*</b>	PQ189757	PQ201945	PQ201944
<i>Pseudopostolata angula</i> <b>gen. et sp. nov.*</b>	PQ189758	PQ201945	PQ201943
<i>Pseudopostolata angula</i> <b>gen. et sp. nov.*</b>	PQ189758	PQ201945	PQ201944
<i>Cosmopseudodon resupinatus</i>	PP079436	PP079964	PP080006
<i>Cosmopseudodon wenshanensis</i>	PP079444	PP079972	PP080014

genera in the subfamily Gonideinae (Fig. 3). This species was identified as the sister group to the focal clade comprising the genera *Postolata*, *Cosmopseudodon*, *Obovalis*, *Ptychorhynchus*, *Parvasolenia*, and *Koreosolenia*. In this clade of Gonideini, the pairwise uncorrected *COI**p*-distance ranged from 11.69% (between this species and *Ptychorhynchus pfisteri* (Heude, 1874)) to 13.58% (between this species and *Koreosolenia sitgyensis* Lee, Kim, Lopes-Lima & Bogan, 2020)) (Table 3), providing compelling evidence for the founding of the new genus (Jeratthitikul et al. 2021; Wu et al. 2022; Dai et al. 2023). Furthermore, this species shows unique morphological characteristics distinguishable from other genera. Therefore, it is described herein as *Pseudopostolata angula* gen. et sp. nov.

Taxonomy

**Family Unionidae Rafinesque, 1820**  
**Subfamily Gonideinae Ortmann, 1916**  
**Tribe Gonideini Ortmann, 1916**

Taxon	COI	16S rRNA	28S rRNA
<b>Pseudodontni Frierson, 1927</b>			
<i>Pseudodon mekongi</i>	KX865861	KX865632	KX865733
<i>Pseudodon vondembuschianus</i>	KP795029	KP795052	MZ684028
<i>Pseudodon cambodjensis</i>	KP795028	NC_044112	KP795011
<i>Bineurus loeiensis</i>	KX865879	KX865650	KX865750
<i>Bineurus mouhotii</i>	KX865876	KX865647	KX865747
<i>Sundadontina tanintharyiensis</i>	MN275057	MN307248	MN307189
<i>Sundadontina brandti</i>	MN275058	MN307249	MN307190
<i>Pilsbryoconcha exilis</i>	KP795024	NC_044124	KP795007
<i>Pilsbryoconcha compressa</i>	KX865875	KX865646	KX865746
<i>Thaiconcha callifera</i>	KX865862	KX865633	KX865734
<i>Thaiconcha munelliptica</i>	MN275063	MN307252	MN307193
<i>Nyeinchanconcha nyeinchani</i>	KP795025	KP795050	KP795008
<b>Lamprotulini Modell, 1942</b>			
<i>Lamprotula caveata</i>	MG462991	NC_030336	MG595518
<i>Lamprotula leaii</i>	MN402616	MN396727	MN396723
<i>Potomida littoralis</i>	MN402617	MN396728	MN396724
<i>Pronodularia japonensis</i>	KX822659	AB055625	KX822615
<b>Chamberlainiini Bogan, Froufe &amp; Lopes-Lima in Lopes-Lima et al., 2017</b>			
<i>Sinohyriopsis schlegelii</i>	MT020706	EF507846	MT020836
<i>Sinohyriopsis cumingii</i>	MG463086	NC011763	MG595613
<i>Chamberlainia hainesiana</i>	KX822635	NC_044110	KX822592
<b>Rectidentini Modell, 1942</b>			
<i>Hyriopsis bialata</i>	KX051274	MT993644	MT993697
<i>Ensidens ingallsianus</i>	MT993541	MT993687	MT993739
<b>Contradentini Modell, 1942</b>			
<i>Lens contradens</i>	MG581991	MT993693	MT993745
<i>Lens comptus</i>	KX865928	KX865682	KX865799
<i>Physunio superbus</i>	MG582020	MT993689	MT993741
<b>Schepmaniini Lopes-Lima, Pfeiffer &amp; Zieritz, 2021</b>			
<i>Schepmania</i> sp.	MZ678755	MZ684082	MZ684035
<b>Ctenodesmini Pfeiffer, Zieritz, Rahim &amp; Lopes-Lima, 2021</b>			
<i>Khairuloconcha lunbawangorum</i>	MN900790	MZ684078	MN902294
<i>Khairuloconcha sahanae</i>	MZ678752	MZ684079	MZ684024
<b>Unioninae Rafinesque, 1820</b>			
<i>Anemina arcaeiformis</i>	NC_026674	NC_026674	MG595457
<i>Cristaria plicata</i>	NC_012716	NC_012716	MG595484
<i>Sinanodonta woodiana</i>	HQ283346	HQ283346	MG595604
<b>MARGARITIFERIDAE Henderson, 1929</b>			
<i>Gibbosula laosensis</i>	JX497731	KC845943	KT343741
<i>Margaritifera margaritifera</i>	KX550089	KX550091	KX550093

**Genus *Pseudopostolata* Dai, Chen, Huang & Wu, gen. nov.**

<https://zoobank.org/4B4557A9-93D2-408E-AC1B-12CF9BDA2D2F>  
Figs 2C, D, 4

**Type species.** *Pseudopostolata angula* Chen, Dai, Huang & Wu, sp. nov.

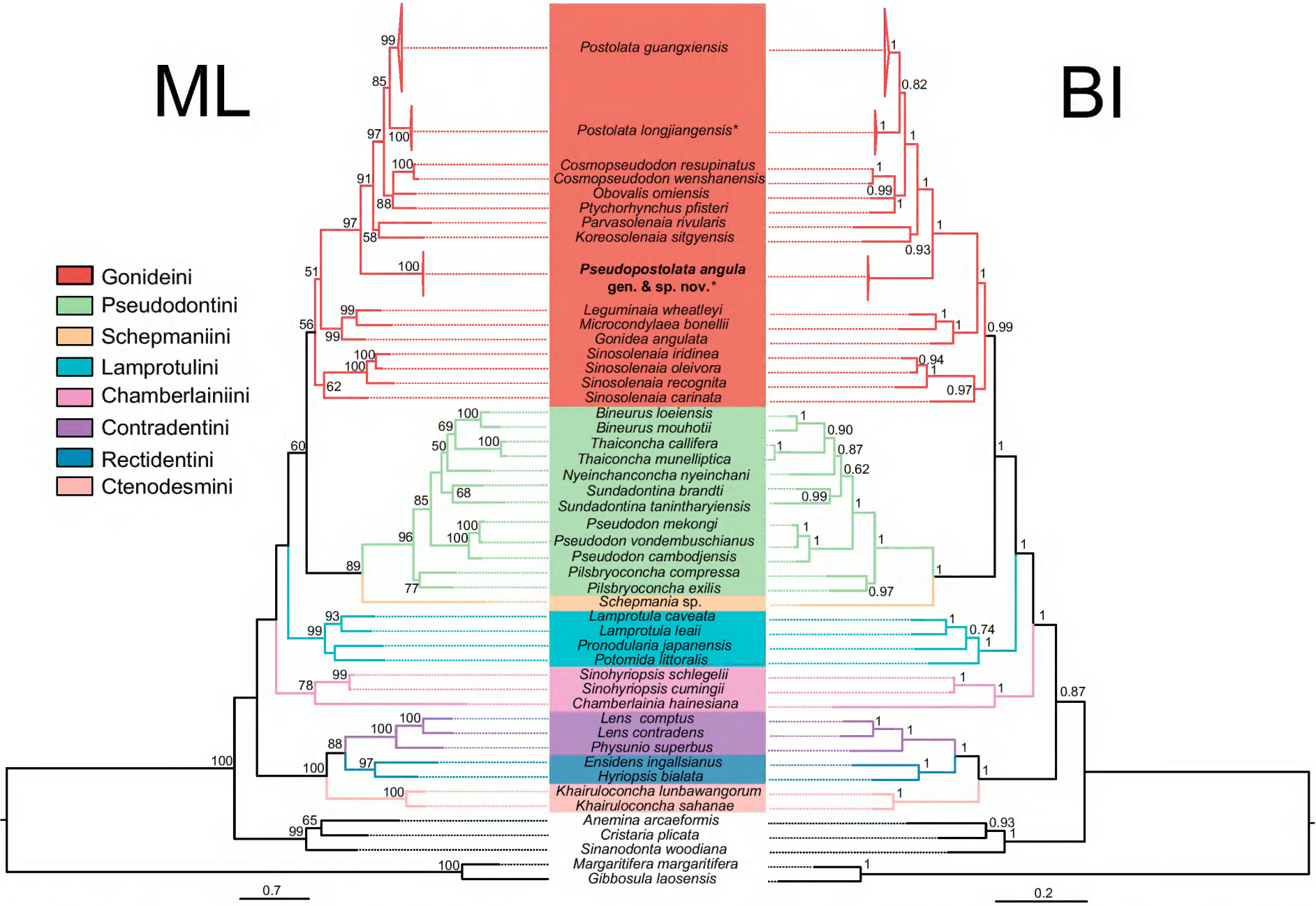
**Diagnosis.** Shell medium size, moderately thick, flat, long, glossy, black without any color rays. Anterior rounded, short, posterior long, and wide. Dorsal margin slightly curved downwards and truncated behind, with a distinct obtuse angle in the middle of posterior margin. Shell surface with a low secondary posterior ridge end in the angle on the posterior margin. Both left and right valves with one or two pseudocardinal teeth.

**Etymology.** The specific name *pseudopostolata* is made from the Latin *pseudo* for false and *postolata* for a unionid genus, alluding to their similar shell morphology.

**Vernacular name.** ‘Pseudorear-wide mussel genus’ (English) and ‘Ni Hou Ju Bang Shu’ (拟后矩蚌属) (Chinese).

**Distribution.** Wujiang River in the Yongfeng section of Jiangxi Province, China.





**Figure 3.** Maximum likelihood (ML) and Bayesian inference (BI) trees of Unionidae based on the three-gene dataset. *Gibbosula laosensis* and *Margaritifera margaritifera* from the family Margaritiferidae were used as outgroup taxa. Maximum likelihood bootstrap support less than 50% or Bayesian posterior probability less than 0.5 were not shown. Taxa marked with an asterisk (\*) were sequenced in this study.

**Remarks.** The new genus belongs to the tribe Gonideini of the subfamily Gonideinae, which currently consists of only one species. The new genus exhibits morphological similarities with *Postolata guangxiensis* Dai, Huang, Guo & Wu, 2023. However, it differs in terms of its elongated shell and the more distinct angle on the posterior margin.

*Pseudopostolata angula* Chen, Dai, Huang & Wu, sp. nov.

<https://zoobank.org/B1F2A547-13E7-47CF-A80B-FF54B9404AB5>  
Figs 2C, D, 4

**Material examined.** *Holotype* • 24\_NCU\_XPWU\_PA01, Wujiang River [乌江], Yongfeng County [永丰县], Ji'an City [吉安市], Jiangxi Province [江西省], China, 27°03'37"N, 115°42'17"E, collected by Zhong-Guang Chen in December 2023; *Paratypes* CHINA • 7 shells; same collection data as for holotype; specimen vouchers were shown in Table 4.

**Diagnosis.** See the diagnosis of the genus.

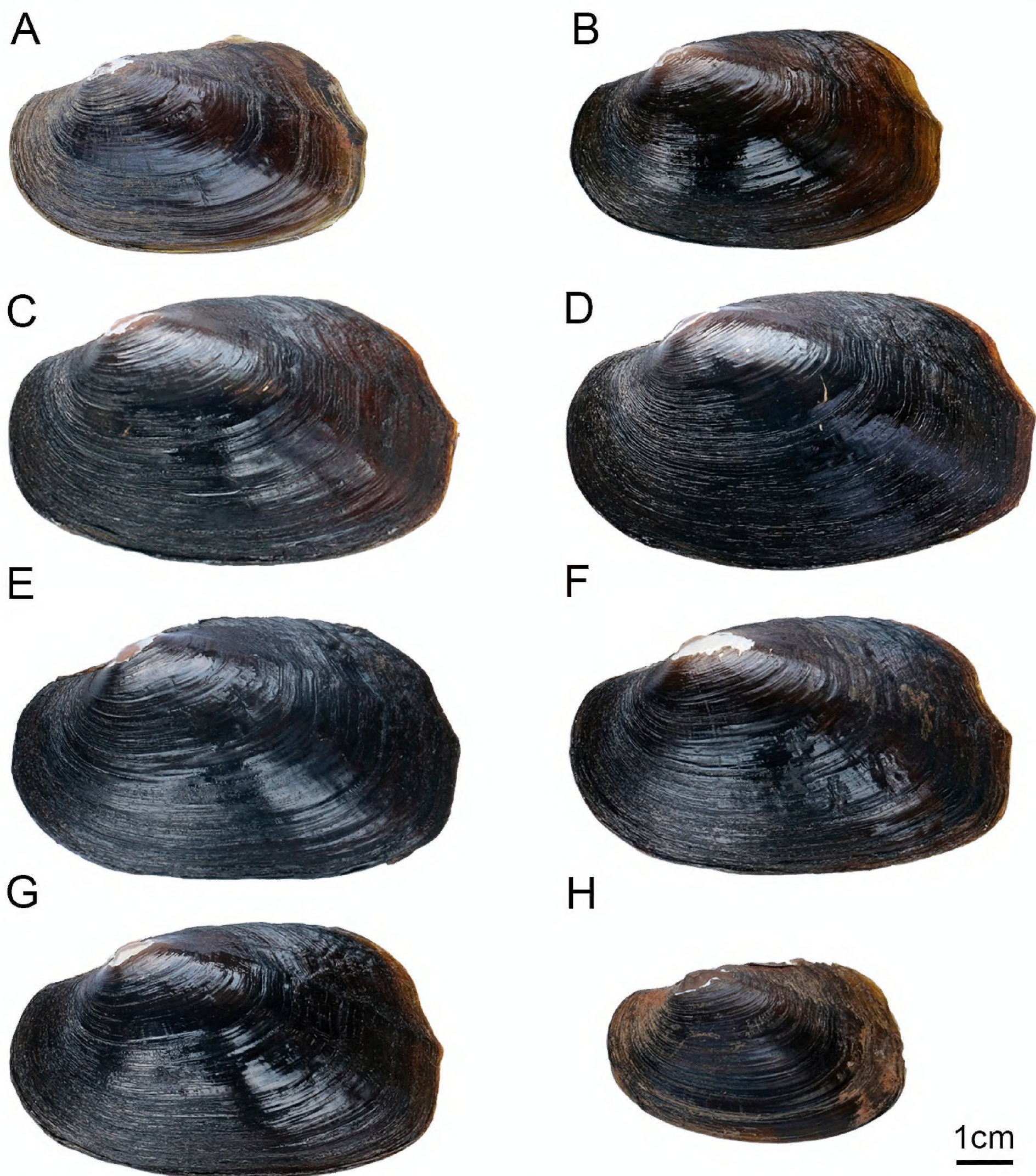
**Description.** Shell medium size, moderately thick, flat, long, glossy. Length 52.16–84.18 mm, width 16.80–25.95 mm, height 32.40–49.53 mm (Table 4). Anterior rounded, short, posterior long, and wide. Dorsal margin

slightly curved downwards and truncated in behind, with a distinct obtuse angle in the middle of posterior margin; ventral margin weakly curved. Umbo inflated, below or even with the hinge line, located at 1/3 of the dorsal margin, and often eroded. Periostracum black with thin growth lines. Posterior slope with a low secondary posterior ridge end in the angle on the posterior margin. Growth lines arranged in irregular concentric circles. Hinge long. Ligament short and strong. Beak cavities shallow, open. Mantle attachment scars on the pallial line obvious. Anterior adductor muscle scars irregularly oval, deep, rough; posterior adductor muscle scars long, oval, smooth. Anterior retractor muscle scar deep; posterior adduster muscle scar shallow, Located obliquely above posterior adductor muscle scars. Left valve with one or two pseudocardinal teeth; anterior tooth elevated pyramidal or degenerated; posterior tooth thick and pyramidal. Right valve also with one or two pseudocardinal teeth; anterior tooth small or elevated pyramidal; posterior tooth low triangular or degenerated. Lateral teeth of both valves long and thick. Nacre light orangish.

**Etymology.** The specific name *angula* is made from the Latin *angula* for angled, alluding to the angle on the posterior margin of this species.

**Vernacular name.** ‘Angulated pseudorear-wide mussel’ (English) and Ju Jiao Ni Hou Ju Bang (具角拟后矩蚌) (Chinese).





**Figure 4.** Eight specimens of *Pseudopostolata angula* gen. et sp. nov. were collected from the Wujiang River in Ji'an City, Jiangxi, China. A is the holotype; A-H responds to specimen vouchers: 24\_NCU\_XPWU\_PA01- 24\_NCU\_XPWU\_PH08.

**Distribution.** *Pseudopostolata angula* sp. nov. is only known from the type locality (Fig. 1).

**Habitat.** This new species was found to occur in the muddy or pebbly substrate of the river together with *Diaurora aurea* (Heude, 1883), *Lanceolaria triformis* (Heude, 1877), *Lamprotula caveata* (Heude, 1877), *Nodularia douglasiae* (Gray, 1833) and *Pseudocuneopsis yangshuoensis* Wu & Liu, 2023 (Fig. 2A, B). It is the occasional species in the habitat, accounting for 5% of the total density of freshwater mussels.

## Discussion

This study integrates morphological and molecular analyses to describe a new genus and species within the Goniideini tribe, which is endemic to the Wujiang River, Jiangxi, China. The newly described genus and species, *Pseudopostolata angula* gen. et sp. nov., shares morphological features typical of Gonideini, including an irregularly rectangular shell (Lopes-Lima et al. 2017; Froufe et al. 2020; Dai et al. 2023). Given the similarities in shell shape, including



**Table 3.** Average intraspecific (bold) and interspecific uncorrected *p*-distance (% ± S.E.) for *COI* sequences of species in Gonideini.

Taxa	1	2	3	4	5	6	7	8	9
1. <i>Pseudopostolata angula</i> <b>gen. et sp. nov.</b>	<b>0.17 ± 0.17</b>								
2. <i>Postolata guangxiensis</i>	12.01 ± 1.31	<b>0.59 ± 0.20</b>							
3. <i>Postolata longjiangensis</i>	12.33 ± 1.32	7.94 ± 1.10	<b>0.17 ± 0.17</b>						
4. <i>Cosmopseudodon wenshanensis</i>	12.92 ± 1.40	10.64 ± 1.28	11.08 ± 1.31	<b>0 ± 0</b>					
5. <i>Cosmopseudodon resupinatus</i>	13.35 ± 1.42	11.41 ± 1.27	11.35 ± 1.31	1.94 ± 0.55	<b>0.09 ± 0.09</b>				
6. <i>Koreosolenia sitgyensis</i>	13.58 ± 1.40	12.14 ± 1.34	12.50 ± 1.39	11.50 ± 1.29	11.50 ± 1.29	0.17 ± 0.16			
7. <i>Obovalis omiensis</i>	12.38 ± 1.33	9.76 ± 1.17	10.67 ± 1.21	10.25 ± 1.23	10.44 ± 1.20	12.96 ± 1.35	1.61 ± 0.36		
8. <i>Parvasolenia rivularis</i>	12.11 ± 1.29	11.71 ± 1.25	12.65 ± 1.35	11.40 ± 1.33	11.65 ± 1.35	11.08 ± 1.24	12.48 ± 1.27	1.23 ± 0.27	
9. <i>Ptychorhynchus pfisteri</i>	11.69 ± 1.31	10.43 ± 1.26	11.53 ± 1.33	8.56 ± 1.14	8.60 ± 1.12	11.61 ± 1.30	9.22 ± 1.16	10.23 ± 1.23	0.59 ± 0.19

**Table 4.** Shell measurements of *Pseudopostolata angula* gen. et sp. nov. Measurements in millimeters (mm).

Status of specimen	Specimen voucher	Shell length	Shell width	Shell height
Holotype	24_NCU_XPWU_PA01	63.29	19.05	37.77
Paratype	24_NCU_XPWU_PA02	52.16	16.80	32.40
Paratype	24_NCU_XPWU_PA03	84.18	25.95	49.16
Paratype	24_NCU_XPWU_PA04	83.55	24.92	49.53
Paratype	24_NCU_XPWU_PA05	80.64	25.38	46.28
Paratype	24_NCU_XPWU_PA06	75.27	22.15	45.68
Paratype	24_NCU_XPWU_PA07	76.67	22.6	45.19
Paratype	24_NCU_XPWU_PA08	62.94	19.31	37.60

a short, rounded anterior and a broad, elongated posterior, this species could easily be mistaken for belonging to the genus *Postolata* Dai, Huang, Guo & Wu, 2023 (Dai et al. 2023). However, further morphological examination revealed distinct characteristics specific to this species. The new genus differs from other genera in Gonideini by its slightly curved dorsal margin, truncated posteriorly with a distinct obtuse angle in the middle of the posterior margin (Fig. 2C, D, Table 5). Additionally, this species exhibits two types of pseudocardinal teeth, which is unique within Gonideini. The first type has two pseudocardinal teeth on both valves; in the left valve, the anterior pseudocardinal tooth is taller than the posterior one, while in the right valve, the anterior pseudocardinal tooth is smaller (Fig. 2C). The second type has a single tall triangular-conical pseudocardinal tooth on both valves; in the left valve, the anterior pseudocardinal tooth is reduced, and in the right valve, the posterior pseudocardinal tooth is reduced (Fig. 2D). The new genus is further distinguished from *Postolata* by its light orange-hued nacre, in contrast to the white nacre of *Postolata*, as well as by its longer shell (Table 5). Given the high prevalence of endemism among freshwater mussels, their taxonomic classification is closely tied to their geographic distribution (Bolotov et al. 2020b; Konopleva et al. 2023). The majority of Gonideini species are found in China, primarily in the Yangtze River Basin, with a few species also present in the Guangxi and Hainan regions (Graf and Cummings 2021; Liu et al. 2024). *Pseudopostolata angula* and *Postolata* are distributed across distinct geographical drainages. The former is endemic to the Yangtze River basin, while the latter, comprising two species (*Postolata guangxiensis* Dai, Huang, Guo & Wu, 2023 and *Postolata longjiangensis* Liu & Wu, 2024), is found in the Pearl River basin (Guangxi) (Dai et al. 2023; Liu et al. 2024). This distinct distribution facilitates a clear differentiation between the two genera.

Five genera within Gonideini, including *Pseudopostolata*, *Postolata*, *Cosmopseudodon*, *Obovalis*, and *Ptychorhynchus*, exhibit a high degree of convergence, with similarities in shell size, shape, and thickness (Table 4). For instance, *Ptychorhynchus murinum* (Heude, 1883) shares a similar shell shape with *Postolata longjiangensis* Liu & Wu, 2024. However, the absence of molecular data for *Ptychorhynchus murinum* precludes a molecular comparison between the two species. Morphologically, *Postolata longjiangensis* is distinguished by fine and dense growth lines on the posterior dorsal, a feature that clearly differentiates it from *Ptychorhynchus murinum*. Additionally, their distinct distributions—*Ptychorhynchus murinum* in the Yangtze River basin and *Postolata longjiangensis* in the Pearl River basin (Guangxi)—further support their differentiation (Graf and Cummings 2021; Liu et al. 2024). Consequently, accurate species identification requires not only useful distinguishing characteristics but also consideration of their distribution, habitat, and a combination of molecular data (Pieri et al. 2018; Jeratthitikul et al. 2022; Bolotov et al. 2023; Dai et al. 2024b). The use of molecular data for DNA taxonomy has shown great promise in expediting the process of species discovery (Huang et al. 2019; Chen et al. 2023). The molecular data results are consistent with morphological analysis. In our multi-locus trees, *Pseudopostolata angula* formed a well-supported monophyletic clade in the tribe Gonideini that did not belong to any previously known species or genera (Fig. 3, Table 3). Furthermore, the considerable genetic divergence from other genera lends additional support to its classification as a distinct genus. (Jeratthitikul et al. 2021; Wu et al. 2022; Dai et al. 2023). The phylogenetic relationships of genera in the focal clade of Gonideini align with previous studies based on *COI* + *16S* rRNA + *28S* rRNA phylogenies (Dai et al. 2023; Liu et al. 2024), although our analysis did not recover the sister relationship between *Ptychorhynchus pfisteri* (Heude, 1874) and *Obovalis omiensis* (Heimburg, 1884) (Fig. 3). Moreover, the phylogenetic analysis revealed that *Parvasolenia rivularis* (Heude, 1877) is sister to *Koreosolenia sitgyensis* Lee, Kim, Lopes-Lima & Bogan, 2020, which contradicts the *COI* + *ND1* + *16S* rRNA + *18S* rRNA + *28S* rRNA phylogeny (Wu et al. 2024). The observed discrepancies between topologies are likely attributable to factors such as incomplete lineage sorting, insufficient taxon sampling, and varying rates of genome evolution and mutation (Perkins et al.



**Table 5.** Analyzed conchological characters of *Pseudopostolata*, *Postolata*, *Cosmopseudodon*, *Ptychorhynchus*, *Obovalis*, *Parvasolenia*, and *Koreosolenia*.

Conchological features	<i>Pseudopostolata</i>	<i>Postolata</i>	<i>Cosmopseudodon</i>	<i>Obovalis</i>	<i>Ptychorhynchus</i>
Shell shape	Irregularly rectangular	Irregularly rectangular	Elongate elliptical	Elongate oval	Elongate elliptical
Shell thickness	Moderately thick	Moderately thick	Moderately thick	Thin	Thin-medium
Umbo	Moderately inflated	Inflated	Moderately inflated	Moderately inflated	Low and flat
Posterior margin	With a distinct obtuse angle in the middle of posterior margin	Almost perpendicular to ventral margin	Weakly curved	Weakly curved	Weakly curved
Surface sculpture	With a low secondary posterior ridge end in the angle on the posterior margin	One sulcus near the posterior dorsal margin	Covered with multiple curved wrinkles and one sulcus	Coarse nodules	Posterior slope sculptured with strong ridges
Pseudocardinal teeth of the left valve	One or two thick and pyramidal teeth	Anterior tooth small, posterior tooth thick and pyramidal	One tooth, thick and Obtuse	One tooth, pyramidal	Two teeth, rather stumpy and roughened
Pseudocardinal teeth of the left valve	One or two thick and pyramidal teeth	Anterior tooth well developed, posterior tooth reduced	One tooth, thick and Obtuse	One tooth, high and triangular	One tooth, blunt
Lateral teeth	One tooth on both valves, long and thick	One tooth on both valves, small and short	One tooth on both valves, weakly developed and short	One tooth on both valves, small and short	1~2 granulous teeth on the left and slightly split up teeth on the right
Nacre colour	Light orangish	White	Bluish-white with an orange umbo pocket	Bluish-white	White

2017). The recognition of higher-level taxa based on poorly supported topologies can give rise to instability in classification systems (Pfeiffer et al. 2019). Phylogenomic analysis will be needed to provide a more robust understanding of the intergeneric relationships within this tribe.

Acknowledgments

This study was supported by the National Natural Science Foundation of China (No. 32360132, No. 32100354) and the Jiangxi Provincial Natural Science Foundation (No. 20232BAB205067).

References

Aldridge DC, Ollard IS, Bepalaya YV, Bolotov IN, Doua K, Geist J, Haag WR, Klunzinger MW, Lopes-Lima M, Mlambo MC, Riccardi N, Sousa R, Strayer DL, Torres SH, Vaughn CC, Zajac T, Zieritz A (2022) Freshwater mussel conservation: A global horizon scan of emerging threats and opportunities. *Global Change Biology* 29(3): 575–589. <https://doi.org/10.1111/gcb.16510>

Bolotov IN, Vikhrev IV, Lopes-Lima M, Lunn Z, Chan N, Win T, Aksenova OV, Gofarov MY, Kondakov AV, Konopleva ES, Tumpeesuwan S (2018) Discovery of *Novaculina myanmarensis* sp. nov. (Bivalvia, Pharidae, Pharellinae) closes the freshwater razor clams range disjunction in Southeast Asia. *Scientific Reports* 8(1): 16325. <https://doi.org/10.1038/s41467-018-05133-4>

Bolotov IN, Kondakov AV, Konopleva ES, Vikhrev IV, Aksenova OV, Aksenov AS, Bepalaya YV, Borovskoy AV, Danilov PP, Dvoryankin GA, Gofarov MY, Kabakov MB, Klishko OK, Kolosova YS, Lyubas AA, Novoselov AP, Palatov DM, Savvinov GN, Solomonov NM, Spitsyn VM, Sokolova SE, Tomilova AA, Froufe E, Bogan AE, Lopes-Lima M, Makhrov AA, Vinarski MV (2020a) Integrative taxonomy, biogeography and conservation of freshwater mussels (Unionidae) in Russia. *Scientific Reports* 10(1): 3072. <https://doi.org/10.1038/s41598-020-59867-7>

Bolotov IN, Konopleva ES, Vikhrev IV, Gofarov MY, Lopes-Lima M, Bogan AE, Lunn Z, Chan N, Win T, Aksenova OV, Tomilova AA, Tanmuangpak K, Tumpeesuwan S, Kondakov AV (2020b)

New freshwater mussel taxa discoveries clarify biogeographic division of Southeast Asia. *Scientific Reports* 10(1): 6616. <https://doi.org/10.1038/s41598-020-63612-5>

Bolotov IN, Konopleva ES, Vikhrev IV, Gofarov MY, Kondakov AV, Lyubas AA, Soboleva AA, Chan N, Lunn Z, Win T, Inkhavilay K (2023) Integrative Taxonomic Reappraisal and Evolutionary Biogeography of the Most Diverse Freshwater Mussel Clade from Southeast Asia (Pseudodontini). *Water* 15(17): 3117. <https://doi.org/10.3390/w15173117>

Castresana J (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular biology and evolution* 17(4): 540–552. <https://doi.org/10.1093/oxfordjournals.molbev.a026334>

Chen ZG, Dai YT, Ouyang S, Huang XC, Wu XP (2023) Unveiling the identity of *Diaurora* Cockerell, 1903 (Bivalvia, Unionidae): morphology, molecular phylogenetics, and the description of a new species. *ZooKeys* 1173: 131–144. <https://doi.org/10.3897/zookeys.1173.106148>

Dai YT, Huang XC, Wu CHZ, Chen ZG, Guo L, Shu FY, Ouyang S, Wu XP (2023) Multilocus and mitogenomic phylogenetic analyses reveal a new genus and species of freshwater mussel (Bivalvia, Unionidae) from Guangxi, China. *Invertebrate Systematics* 37(2): 152–166. <https://doi.org/10.1071/is22048>

Dai YT, Chen ZG, Hu CL, Ning PF, Ouyang S, Huang XC, Wu XP, Giribet G (2024a) Taxonomic reassessment of *Scabies* (Bivalvia, Unionidae) species in China based on multilocus and mitogenomic phylogenetic analyses. *Invertebrate Systematics* 38(6): IS24020. <https://doi.org/10.1071/is24020>

Dai YT, Chen ZG, Peng KJ, Ouyang S, Huang XC, Wu XP (2024b) Revisiting the genus *Pseudocuneopsis* (Bivalvia, Unionidae): Morphology, mitochondrial phylogenomics, and the description of a new species. *Zoologica Scripta* 53(3): 323–337. <https://doi.org/10.1111/zsc.12647>

Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32(5): 1792–1797. <https://doi.org/10.1093/nar/gkh340>

Edler D, Klein J, Antonelli A, Silvestro D, Matschiner M (2020) raxml-GUI 2.0: A graphical interface and toolkit for phylogenetic analyses using RAxML. *Methods in Ecology and Evolution* 12(2): 373–377. <https://doi.org/10.1111/2041-210x.13512>

Froufe E, Bolotov I, Aldridge DC, Bogan AE, Breton S, Gan HM, Kovitvadhi U, Kovitvadhi S, Riccardi N, Secci-Petretto G, Sousa



- R, Teixeira A, Varandas S, Zanatta D, Zieritz A, Fonseca MM, Lopes-Lima M (2020) Mesozoic mitogenome rearrangements and freshwater mussel (Bivalvia, Unionoidea) macroevolution. *Heredity* 124(1): 182–196. <https://doi.org/10.1038/s41437-019-0242-y>
- Graf DL, Cummings KS (2021) A ‘big data’ approach to global freshwater mussel diversity (Bivalvia, Unionoida), with an updated checklist of genera and species. *Journal of Molluscan Studies* 87(1): eyaa034. <https://doi.org/10.1093/mollus/eyaa034>
- Haag WR (2012) North American freshwater mussels: natural history, ecology, and conservation. Cambridge University Press, UK. <https://doi.org/10.1017/CBO9781139048217>
- Huang XC, Su JH, Ouyang JX, Ouyang S, Zhou CH, Wu XP (2019) Towards a global phylogeny of freshwater mussels (Bivalvia, Unionida): Species delimitation of Chinese taxa, mitochondrial phylogenomics, and diversification patterns. *Molecular Phylogenetics and Evolution* 130: 45–59. <https://doi.org/10.1016/j.ympev.2018.09.019>
- Inoue K, Hayes DM, Harris JL, Christian AD (2013) Phylogenetic and morphometric analyses reveal ecophenotypic plasticity in freshwater mussels *Obovaria jacksoniana* and *Villosa arkansasensis* (Bivalvia, Unionidae). *Ecology and Evolution* 3(8): 2670–2683. <https://doi.org/10.1002/ece3.649>
- Jeratthitikul E, Sutcharit C, Ngor PB, Prasankok P (2021) Molecular phylogeny reveals a new genus of freshwater mussels from the Mekong River Basin (Bivalvia, Unionidae). *European Journal of Taxonomy* 775: 119–142. <https://doi.org/10.5852/ejt.2021.775.1553>
- Jeratthitikul E, Paphatmethin S, Sutcharit C, Ngor PB, Inkhavilay K, Prasankok P (2022) Phylogeny and biogeography of Indochinese freshwater mussels in the genus *Pilsbryoconcha* Simpson, 1900 (Bivalvia, Unionidae) with descriptions of four new species. *Scientific Reports* 12(1): 20458. <https://doi.org/10.1038/s41598-022-24844-9>
- Katoh K, Rozewicki J, Yamada KD (2019) MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics* 20(4): 1160–1166. <https://doi.org/10.1093/bib/bbx108>
- Konopleva ES, Bolotov IN, Vikhrev IV, Inkhavilay K, Gofarov MY, Kondakov AV, Tomilova AA, Chapurina YE, Van Do T, Pfeiffer JM, Lopes-Lima M, Bogan AE (2023) A freshwater mussel species reflects a Miocene stream capture between the Mekong Basin and East Asian rivers. *Zoosystematics and Evolution* 99(1): 29–43. <https://doi.org/10.3897/zse.99.90784>
- Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution* 35(6): 1547–1549. <https://doi.org/10.1093/molbev/msy096>
- Lanfear R, Frandsen PB, Wright AM, Senfeld T, Calcott B (2017) PartitionFinder 2: New Methods for Selecting Partitioned Models of Evolution for Molecular and Morphological Phylogenetic Analyses. *Molecular Biology and Evolution* 34(3): 772–773. <https://doi.org/10.1093/molbev/msw260>
- Liu L, Zhang L, Hou K, Ning L, Wu R (2024) Addition to the known diversity of Chinese freshwater mussels: integrative description of a new species of *Postolata* Dai et al., 2023 (Bivalvia, Unionidae, Gonideinae). *Zoosystematics and Evolution* 100(3): 769–778. <https://doi.org/10.3897/zse.100.126069>
- Lopes-Lima M, Froufe E, Do VT, Ghamizi M, Mock KE, Kebapci Ü, Klishko O, Kovitvadhi S, Kovitvadhi U, Paulo OS, Pfeiffer JM, Raley M, Riccardi N, Şereflişan H, Sousa R, Teixeira A, Varandas S, Wu XP, Zanatta DT, Zieritz A, Bogan AE (2017) Phylogeny of the most species-rich freshwater bivalve family (Bivalvia, Unionida, Unionidae): Defining modern subfamilies and tribes. *Molecular Phylogenetics and Evolution* 106: 174–191. <https://doi.org/10.1016/j.ympev.2016.08.021>
- Park JK, Foighil DÓ (2000) Sphaeriid and Corbiculid Clams Represent Separate Heterodont Bivalve Radiations into Freshwater Environments. *Molecular Phylogenetics and Evolution* 14(1): 75–88. <https://doi.org/10.1006/mpev.1999.0691>
- Perkins MA, Johnson NA, Gangloff MM (2017) Molecular systematics of the critically-endangered North American spinymussels (Unionidae, Elliptio and Pleurobema) and description of *Parvaspina* gen. nov. *Conservation Genetics* 18(4): 745–757. <https://doi.org/10.1007/s10592-017-0924-z>
- Pfeiffer JM, Breinholt JW, Page LM (2019) Unioverse: A phylogenomic resource for reconstructing the evolution of freshwater mussels (Bivalvia, Unionoida). *Molecular Phylogenetics and Evolution* 137: 114–126. <https://doi.org/10.1016/j.ympev.2019.02.016>
- Pieri AM, Inoue K, Johnson NA, Smith CH, Harris JL, Robertson C, Randklev CR (2018) Molecular and morphometric analyses reveal cryptic diversity within freshwater mussels (Bivalvia, Unionidae) of the western Gulf coastal drainages of the USA. *Biological Journal of the Linnean Society* 124(2): 261–277. <https://doi.org/10.1093/biolinnean/bly046>
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61(3): 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Rozas J, Ferrer-Mata A, Sanchez-DelBarrio JC, Guirao-Rico S, Librado P, Ramos-Onsins SE, Sanchez-Gracia A (2017) DnaSP 6: DNA Sequence Polymorphism Analysis of Large Data Sets. *Molecular Biology and Evolution* 34(12): 3299–3302. <https://doi.org/10.1093/molbev/msx248>
- Smith CH, Johnson NA, Inoue K, Doyle RD, Randklev CR (2019) Integrative taxonomy reveals a new species of freshwater mussel, *Potamilus streckersoni* sp. nov. (Bivalvia, Unionidae): implications for conservation and management. *Systematics and Biodiversity* 17(4): 331–348. <https://doi.org/10.1080/14772000.2019.1607615>
- Sousa R, Zając T, Halabowski D, Aksenova OV, Bespalaya YV, Carvalho F, Castro P, Douda K, da Silva JP, Ferreira-Rodríguez N, Geist J, Gumpinger C, Labecka AM, Lajtner J, Lewin I, Lopes-Lima M, Meira A, Nakamura K, Nogueira JG, Ondina P, Özgo M, Reis J, Riccardi N, Shumka S, Son MO, Teixeira A, Thielen F, Urbańska M, Varandas S, Wengström N, Zając K, Zieritz A, Aldridge DC (2022) A roadmap for the conservation of freshwater mussels in Europe. *Conservation Biology* 37(2): e13994. <https://doi.org/10.1111/cobi.13994>
- Walker JM, Bogan AE, Bonfiglio EA, Campbell DC, Christian AD, Curole JP, Harris JL, Wojtecki RJ, Hoeh WR (2007) Primers for amplifying the hypervariable, male-transmitted COII-COI junction region in amblesine freshwater mussels (Bivalvia, Unionoidea, Amblesinae). *Molecular Ecology Notes* 7(3): 489–491. <https://doi.org/10.1111/j.1471-8286.2006.01630.x>
- Wu XP, Dai YT, Yin N, Shu FY, Chen ZG, Guo L, Zhou CH, Ouyang S, Huang XC (2022) Mitogenomic phylogeny resolves *Cuneopsis* (Bivalvia, Unionidae) as polyphyletic: The description of two new genera and a new species. *Zoologica Scripta* 51(2): 173–184. <https://doi.org/10.1111/zsc.12527>



- Wu RW, Liu LL, Zhang LP, Jia JL, Jin DD, Wu XP, Liu XJ (2023) New species of the genus *Pseudocuneopsis* Huang, Dai, Chen & Wu, 2022 (Bivalvia, Unionidae) from Guangxi Province, China. *ZooKeys* 1166: 261–270. <https://doi.org/10.3897/zookeys.1166.104150>
- Wu R, Liu L, Zhang L, Bogan AE, Niu G, Jin D, Wu X, Liu X (2024) Taxonomic revision of two species in the genus *Ptychorhynchus* Simpson, 1900 (Bivalvia, Unionidae, Gonideinae), with description of a new species. *Invertebrate Systematics* 38: IS24014. <https://doi.org/10.1071/IS24014>
- Zieritz A, Aldridge D (2009) Identification of ecophenotypic trends within three European freshwater mussel species (Bivalvia, Unionoida) using traditional and modern morphometric techniques. *Biological Journal of the Linnean Society* 98(4): 814–825. <https://doi.org/10.1111/j.1095-8312.2009.01329.x>
- Zieritz A, Bogan AE, Froufe E, Klishko O, Kondo T, Kovitvadhi U, Kovitvadhi S, Lee JH, Lopes-Lima M, Pfeiffer JM, Sousa R, Van Do T, Vikhrev I, Zanatta DT (2018) Diversity, biogeography and conservation of freshwater mussels (Bivalvia, Unionida) in East and Southeast Asia. *Hydrobiologia* 810: 29–44. <https://doi.org/10.1007/s10750-017-3104-8>
- Zieritz A, Pfeiffer J, Rahim KAA, Prayogo H, Anwari MS, Diba F, Froufe E, Blackwell T, Hartikainen H, Lopes-Lima M (2024) High endemic freshwater mussel (Bivalvia, Unionida) diversity in western Borneo, with description of three new species. *Zoological Journal of the Linnean Society* 201(3): zlae076. <https://doi.org/10.1093/zoolinnean/zlae076>
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